



Insect noise avoidance in the dawn chorus of Neotropical birds



Calandra Q. Stanley^{a,*}, Michael H. Walter^b, Madhvi X. Venkatraman^a,
Gerald S. Wilkinson^a

^a Department of Biology, University of Maryland, College Park, MD, U.S.A.

^b Animal Physiology, Institute for Neurobiology, University of Tübingen, Germany

ARTICLE INFO

Article history:

Received 17 May 2015

Initial acceptance 22 June 2015

Final acceptance 23 October 2015

Available online

MS. number: A15-00412R

Keywords:

acoustic partitioning
ambient noise
animal communication
Barro Colorado Island
birdsong
cicada
signal active space

Many species of birds conspicuously call or sing early in the morning, thereby creating an avian dawn chorus. While these vocalizations probably function to advertise territory occupancy, when species should start singing is not well understood. A common explanation is that birds sing at dawn to maximize signal transmission due to low atmospheric turbulence during the early morning (acoustic transmission hypothesis); however, this idea does not explain why species in the chorus often start singing at different times. Here we test a version of this hypothesis: interspecific differences in call start times during the dawn chorus are a result of noise avoidance at the song's frequency. To test this hypothesis we quantified the spectral and temporal properties of the dawn chorus and the acoustic landscape at Barro Colorado Island, Panama. Inspection of 36 dawn recordings at 12 sites identified 27 species of birds, with most species having consistent start times across sites and days. In contrast to expectations, we found that birds singing within the same frequency range did not temporally partition acoustic space during the chorus. Discriminant function analysis revealed that nearly all species in the chorus produced distinctive vocalizations. Surprisingly, song start time was positively related to peak frequency. Birds with high-frequency vocalizations did not begin singing until after orthopteran insects stopped producing loud sounds at the same frequencies. These results suggest that birds that sing at frequency bands shared by nocturnal insects avoid acoustic masking by delaying song start times. Playbacks of emerald cicada, *Zammara smaragdina*, buzzes conducted during the dawn chorus produced an inhibitory effect on the call activity of birds singing within the bandwidth of cicada calls. Thus, insect noise appears to create an important frequency-dependent constraint on the calling activity of birds. This constraint is overcome by temporal partitioning of acoustic space.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

The dawn chorus occurs during a short period of the morning when most members of the avian community call or sing together. This daily occurrence is so regular that numerous species have been reported to begin singing at characteristic times every morning (Allard, 1930; Leopold & Eynon, 1961). Although often pleasing to the human ear, this cacophony creates a dilemma for all participants: when should an individual sing in order to be heard most clearly? Given the important role that song plays in both territory defence and mate acquisition for birds, being heard by conspecifics should have direct fitness advantages, leading to selection for mechanisms to ensure detection and discrimination of individuals (Endler, 1992; Wiley, 2006). Consequently, species-specific signals that are sufficiently different in spectral or temporal features to

avoid interference and signal masking within the acoustic community are expected to evolve (Endler, 1993; Wiley, 2006). In addition to avoiding heterospecific interference, birds must also compete for acoustic space from other sources of noise (e.g. wind, insect, anthropogenic; Brumm & Slabbekoorn, 2005). This can be particularly challenging in some habitats, such as tropical rainforests, where dense vegetation interferes with long-distance signalling and species from a variety of taxa produce sounds (Luther, 2009; Ryan & Brenowitz, 1985; Slabbekoorn, 2004). This combination of high acoustic diversity and restricted calling period provides an excellent setting in which to examine the mechanisms used by animals to increase the overall active space of their signal and ensure effective communication.

Ambient noise has long been considered an important constraint on avian acoustic signal design (Brenowitz, 1982; Brumm & Slabbekoorn, 2005; Ryan & Brenowitz, 1985; Wiley, 1994, 2006). Heterospecific birdsong can be a common source of acoustic

* Correspondence: C. Q. Stanley, Department of Biology, University of Maryland, College Park, MD 20742, U.S.A.

E-mail address: callie@umd.edu (C. Q. Stanley).

interference, and evidence of acoustic space partitioning has been found in Neotropical avian assemblages (Luther, 2009; Planqué & Slabbekoorn, 2008). In addition, nonavian noise can have an equally important influence on the transmission and reception of avian acoustic signals. In particular, some bird species adjust both the spectral and temporal properties of their songs to minimize overlap with anthropogenic noise in urban environments (e.g. Brumm, 2004; Fuller, Warren, & Gaston, 2007; Wood & Yezerinac, 2006). Tropical forests are another habitat with high background noise that can be heterogeneous in space, time and frequency, creating a complex acoustic landscape in which animals have to communicate (Luther & Gentry, 2013; Rodriguez et al., 2014). Many tropical animals use sound for communication, including various insects, such as orthopterans (crickets and katydids) and hemipterans (cicadas), as well as various nonavian vertebrates including frogs and mammals. Many insect sounds are loud, exhibit frequency overlap with some bird sounds and vary temporally with a peak at night and cessation at sunrise (Diwakar & Balakrishnan, 2007; Lang, Teppner, Hartbauer, & Römer, 2005). Such nonavian noise has considerable potential to interfere with avian communication at dawn but has received comparatively little study.

How selection operates on the timing of acoustic signals and particularly why dawn chorus is such a widely employed strategy of communication remain open questions. Three nonmutually exclusive hypotheses have been proposed to describe why birds sing at dawn. The acoustic transmission hypothesis posits that dawn is the best time of day for the propagation and discrimination of acoustic signals due to favourable temperature, humidity and wind (Brenowitz, 1982; Brown & Handford, 2003; Henwood & Fabrick, 1979). The energy storage stochasticity hypothesis predicts that the optimal time for a bird to sing is at dawn (and dusk) in order to take advantage of energy reserves remaining from the previous night (owing to unpredictable overnight energy requirements; Hutchinson, 2002; McNamara, Mace, & Houston, 1987). The inefficient foraging hypothesis links the timing of dawn chorus to light availability (Berg, Brumfield, & Apanius, 2006; Thomas et al., 2002) and predicts that dawn choruses occur in the interim low-light period between when birds are first able to initiate territorial advertisements and when they are able to forage effectively (Armstrong, 1963; Kacelnik, 1979; Krams, 2001). The inefficient foraging hypothesis is the only hypothesis that has been used to address the staggered start time of different species during a dawn chorus, linking eye size (a measure of a species' ability to see in low light) to song start time (Berg et al., 2006; Thomas et al., 2002). At a community level, the acoustic transmission hypothesis has found support explaining the timing of the dawn chorus, since low air turbulence at dawn maximizes sound propagation and decodability (Brown & Handford, 2003; Henwood & Fabrick, 1979). It has not, by contrast, been used to explain interspecific differences in song start times, as atmospheric conditions are expected to be similar for most, if not all, species in an assemblage. However, other factors, such as ambient noise, do vary across time and frequency and could potentially result in species-specific periods when the active space of a call is maximal.

In this paper we examine when birds join the dawn chorus in a Neotropical rainforest. In particular we investigate an expanded version of the acoustic transmission hypothesis to determine whether ambient noise that has the potential to reduce signal detection and discrimination could explain interspecific differences in song start times during the dawn chorus. We evaluate whether different bird species disperse their calls or songs in acoustic space to avoid spectral or temporal overlap with each other or with other noise in the environment. We predicted that birds join a chorus at different times to avoid temporal overlap with both avian and nonavian noise at their song frequency. We also experimentally

assessed whether some species of birds avoid nonavian noise by altering their singing behaviour. Cicadas produce long, broadband signals that dominate the acoustic background in tropical lowland forests during the day (Nischk & Riede, 2001). By simulating cicada noise using playbacks, we tested whether birds actively avoid insect noise when it occurs at their song frequency through an immediate change in singing activity.

METHODS

Ethical Note

This study was approved by the University of Maryland Institutional Animal Care and Use Committee (579030-1) and by the Smithsonian Tropical Research Institute (2014-0815-2017).

Study Site and Recording Methods

Audio recordings of the dawn chorus were made over a 2-week period during the wet season (late August, 2014) on Barro Colorado Island (BCI), Panama (9°09'N, 79°51'W). BCI is a 1562 ha land-bridge island located in Gatun Lake within the Panama Canal. The island has been isolated from the mainland since the Panama Canal was formed in 1911 and consists of secondary forest with areas of less disturbed old growth forest (Willis, 1974). Average annual precipitation at BCI is approximately 2960 mm, and the life zone is characterized as tropical moist forest (Holdridge, 1967). We conducted a total of 36 hour-long recordings at 12 sites located in secondary forest on the eastern half of the island, at least 300 m from occupied buildings (Supplementary Fig. S1). We visited each site twice within a 2-week period to record ambient sounds at dawn with a single recording unit. In addition, we visited six of these sites with two recording units to monitor responses to cicada playbacks as described below. We started 30 min before nautical twilight and recorded for 1 h to capture the first calls of birds joining the dawn chorus. Recordings were not made in the rain.

We used four ZOOM H2n Handy Recorders (Tokyo, Japan) connected to Sennheiser ME 66 microphones with a flat frequency response between 200 and 6000 Hz (± 2 dB) to make recordings. During each recording period we continuously monitored sound levels and pointed microphones towards vocalizing birds. The Sennheiser ME 66 is directional in that sounds within 30° of where the microphone is aimed are recorded ± 2 dB while sounds 90° or greater away are reduced by 10 dB or more. Consequently, the directional sensitivity of the microphones allowed us to identify species from distant calls despite background noise and generate high-quality spectrograms for species identification and acoustic measurements. Files were digitized at 16 bits with a sampling frequency of at least 44.1 kHz and saved in WAV format. On day 1, we manually adjusted the input gain while recording. On day 2 and onwards we set the input gain of the four recording units to the maximum, which significantly improved the maximum range of each recording unit. Therefore, the files obtained from the first day were used only for call identification and not for quantifying relative changes of background noise during the dawn chorus. We did not attempt to measure absolute amplitude values of ambient noise. Reported noise values are, therefore, relative to the maximum input amplitude of the microphone–recorder combination (ca. 120 dB).

Call and Noise Measurements

We counted calls by listening to recordings and analysing spectrograms created by Raven Pro v.1.4 (<http://www.birds.cornell.edu/brp/raven/ravenversions>) using a Hann window, FFT = 4096 and

50% overlap. We identified the species of bird that produced each call by comparing sounds and spectrograms to recordings available from Xeno-Canto (www.xeno-canto.org) and the Macaulay Library (Cornell University, Ithaca, NY, U.S.A.) and then created a library of audio and spectrogram samples for each species. Species identifications (see [Appendix, Table A1](#)) were confirmed by expert field guides that were conducting point counts on BCI. For each recording session we counted the number of discrete calls recorded for each species in each 5 min time period or for species with continuous calls, such as crested guan, *Penelope purpurascens*, and mealy amazon parrot, *Amazona farinosa*, we counted the number of seconds in which calls occurred. We also noted the time at which the first call of each species occurred for every recording session. While some nocturnal species, such as owls, were identified in the recordings, only diurnal species are included in our analyses.

To quantify acoustic features of calls and background noise, we used Selena, a custom-made sound analysis program developed at the University of Tübingen (Tübingen, Germany). For each species we selected at least three (mean \pm SE = 17.7 ± 2.4) calls with high signal-to-noise ratio for analysis. We used calls from different recording sites and units whenever possible to capture interindividual differences in call features. Using Selena we computed spectrograms (Blackman window, FFT = 2048, variable overlap) with a dynamic range of 80 dB and extracted or calculated the following acoustic features from each call: (1) duration (ms), (2) minimum, (3) maximum frequency, (4) peak frequency (the frequency in Hz with the highest amplitude in the power spectrum), (5) bandwidth (maximum minus minimum frequency), (6) number of notes, (7) complexity (bandwidth divided by duration) and (8) note rate (number of notes divided by duration). Number of notes was manually counted by inspection of the spectrogram. Measurements of complexity and note rate follow [Luther \(2009\)](#). We used the harmonic of the call with the most energy for all measurements. For species that produced multiple types of vocalizations (e.g. cocoa woodcreeper, *Xiphorhynchus susurrans*), we only used the most common call type for analysis. We analysed a total of 477 calls (see [Supplementary Table S1](#) for summaries of call feature measurements).

We investigated the change in nonavian noise level over the course of the morning by splitting each 1 h recording into 12 equal 5 min bins. Each bin was visualized in Selena as a spectrogram (Blackman window, FFT = 512, 14.2% overlap) with a dynamic range of 90 dB. To quantify nonavian noise, we chose a 5 s interval lacking bird calls, when possible, approximately in the middle of each bin and calculated a mean power spectrum. We then used Selena to calculate the mean noise amplitude across all frequencies in discrete steps. The size of each frequency step is half the sampling frequency divided by FFT size (i.e. $22\,050/512 = 43$ Hz). We exported the mean amplitudes of all frequency steps for each of the 12 time bins. As noted above, all amplitude values are relative to the highest possible input amplitude of the recording system. By taking averages across sites, any change in background noise over time cannot be due either to site or to recording unit.

Playbacks

We determined whether birds respond to insect noise by conducting playback trials using recordings of emerald cicadas, *Zammarasp smaragdina*, that we made during morning recording sessions. This species of cicada produces a loud, broadband oscillatory sound that extends from 2.5 to 16 kHz (see [Fig. 1](#)). A single calling bout typically lasts 10–15 s, but individual cicadas can call repeatedly for 1 min or longer (see [Supplementary Fig. S2](#)). Cicada calls were recorded at all 12 sites although not on every day. Recorded cicada calling bout number ranged from 1 to 18 in a 5 min period. Average

time of first recorded cicada call was 3 min before dawn, but ranged from 9 min before to 8 min after dawn. Consequently, we made a playback stimulus that consisted of five consecutive calling bouts, which lasted approximately 1 min. Using a smartphone connected wirelessly to a portable loud speaker (JAM Wireless Speaker, Model HX-P230) placed 1 m above ground, we broadcast the 1 min cicada calls at 5 min intervals starting 30 min before dawn and continuing until 30 min after dawn. During playback trials, two recordings were made facing in opposite directions from the loud speaker, which was 20 m from each microphone. Subsequent inspection of those recordings revealed that playbacks were indistinguishable from natural cicada calls (cf. [Fig. 1, Supplementary Fig. S2](#)) and that bird calls were sometimes detected on only one of the paired recordings. Therefore, we used the maximum number of calls counted in either recording to score potential responses by seven common species. Playback trials were conducted at six different sites. On the same day as a playback trial, recordings were made at two other sites to determine whether the presence of playbacks at a site influenced calling activity of any species.

Statistical Analyses

To assess whether birds call at different times to avoid frequency overlap with each other, we plotted the absolute difference in peak frequency against the absolute difference in average calling time for all possible pairwise species combinations. Average calling time was calculated as the sum of the products of the number of calls counted during each 5 min period multiplied by the midpoint of the period (expressed as a deviation from sunrise in minutes), divided by the total number of calls for each species. For example, for the crimson-crested woodpecker, *Campephilus melanoleucos*, we recorded one call in the time interval -12.5 min, four calls in the time interval $+22.5$ min and three calls in the time interval $+27.5$ min. The sum of these products divided by the total number of calls is $+20$ min ($160/8$). Therefore, the average calling time of the crimson-crested woodpecker was 20 min after sunrise (0630 hours). A negative relationship between these two variables is expected if species with calls that span similar frequencies tend to call at different times of the day. We assessed the significance of this correlation with a Mantel test using the *vegan* package ([Oksanen et al., 2013](#)) in R.

To determine whether calls from different species are distinguishable using more than just frequency information, we performed a quadratic discriminant function analysis on three minimally correlated acoustic traits (peak frequency, bandwidth/call duration and number of notes/call duration) and scored the number of calls that were classified correctly.

We identified factors that predicted the time at which each species of bird began to sing by fitting a series of linear models using the following five factors as possible explanatory variables: (1) peak frequency of the song, (2) noise avoidance at frequency and time of first song relative to the entire morning, (3) singing location (scored as in canopy or below canopy), (4) diet (scored as insectivorous or other) and (5) body mass (see [Supplementary Table S2](#) for summary of species characteristics). Noise avoidance was calculated for each species by subtracting nonavian noise (as described above) at the time and frequency bin that contained their first call from the average noise (calculated over all other time bins at that frequency step). Given that the goal of the analysis was to determine whether birds actively avoid noise that would mask their songs, we chose the frequency step that included the species' peak frequency for this analysis as an approximation of masking potential. The maximum deviation between the frequency step used and the actual peak frequency was 21 Hz. All results are reported as the mean over all days and sites unless stated otherwise.

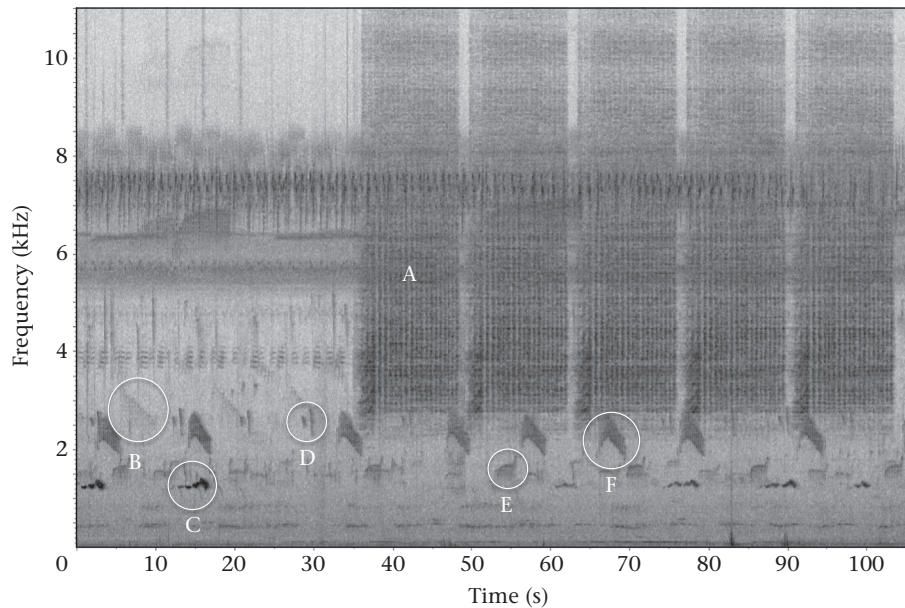


Figure 1. Typical spectrogram (FFT = 4096) of a recording made at dawn. Letters indicate (A) a cicada playback and songs of (B) white-flanked antwren, (C) great tinamou, *Tinamus major*, (D) chestnut-backed antbird, (E) western slaty antshrike and (F) cocoa woodcreeper. Bands of nonavian insect noise are visible between 4 and 8 kHz.

We included singing location to determine whether birds foraging in the canopy sing earlier because there is more light (inefficient foraging hypothesis) and we included diet because birds feeding primarily on animals or fruits would require different light levels for feeding to be profitable (inefficient foraging hypothesis). Body mass was included because larger birds are expected to be more resistant to fasting overnight, leaving more energy reserves in the morning to sing prior to feeding (energy storage stochasticity hypothesis). Information on body mass, location and diet were obtained from [Stiles, Skutch, and Gardner \(1989\)](#). We weighted species by the number of sites where each species was recorded to reflect the amount of information that contributed to each value. We then considered all possible models with main effects or two-way interactions and used Akaike's Information Criterion (corrected for small samples, AICc) to identify the best-fitting model.

To assess the effect of cicada playbacks on singing activity, we conducted two different analyses. First, songs of seven commonly recorded species were counted 1 min before, 1 min during and 1 min after each cicada playback. We then compared the number of songs counted during a playback to those counted after the playback, both expressed as deviations from the number counted before the playback, for each species using paired *t* tests. Second, total songs (or seconds of songs) were tallied for each bird at each site on days when cicada playbacks were and were not conducted. Then, we performed a mixed model ANOVA using total song counts from days on which playbacks were performed and treating date as a random effect and playback as a fixed effect for each species of bird that was recorded. We used a sequential Bonferroni correction to adjust alpha for multiple testing.

Unless stated otherwise, all statistical analyses were conducted using JMP v.10.0.2 (SAS Institute, Cary, NC, U.S.A.).

RESULTS

Song Patterns During the Dawn Chorus

Inspection of the average number of singing events counted per site and 5 min interval revealed that the recording sessions

successfully captured the peak of the dawn chorus. The average number of singing events increased until 12.5 min after sunrise, when number of singing events reached a maximum before declining ([Fig. 2a](#)). In total we counted 76 508 vocalizations from 27 species in 15 families and nine orders (see [Appendix Table A1](#) for common and scientific names, as well as the four-letter code for each species). The number of species recorded at any one site varied from 17 to 25, 11 species were recorded at all 12 sites, and each species was recorded on at least 3 days ([Supplementary Table S3](#)). Average time of first song was very consistent for most species across sites and days, with collared forest-falcons, *Micrastur semitorquatus*, invariably singing first 25 min before dawn, and red-capped manakins, *Ceratopipra mentalis*, not singing until 15 min after dawn ([Fig. 2b](#)). First call time was, therefore, reliably measured by these data.

No significant correlation was found between the absolute difference in peak frequency and the absolute difference in average call activity (Mantel: $r = 0.141$, $P = 0.094$; [Supplementary Fig. S3](#)). In fact, the trend was positive, suggesting that species with songs of similar frequency tended to sing at similar times rather than at different times. A discriminant function analysis correctly classified 99.4% of 477 calls to species on the basis of three spectrotemporal features ([Fig. 3](#)). All three misclassifications involved white-flanked antwren, *Myrmotherula axillaris*, and blue-black grosbeak, *Cyanocopsa cyanooides*. The three discriminant functions accounted for 70.8%, 18.0% and 11.1% of the variation, respectively. The first discriminant function (DF1) was weighted primarily by peak frequency while DF2 and DF3 were influenced primarily by bandwidth/duration and notes/duration ([Table 1](#)). Thus, most species did not overlap in peak frequency, but those that did overlap differed sufficiently in song rate or complexity to remain distinctive even when they called simultaneously during a dawn chorus.

Nonavian Noise During the Dawn Chorus

During the dawn chorus, nonavian noise was consistent across sites but highly variable over time. We observed pronounced changes in several distinct frequency bands where noise was high early in the morning and then gradually decreased over time

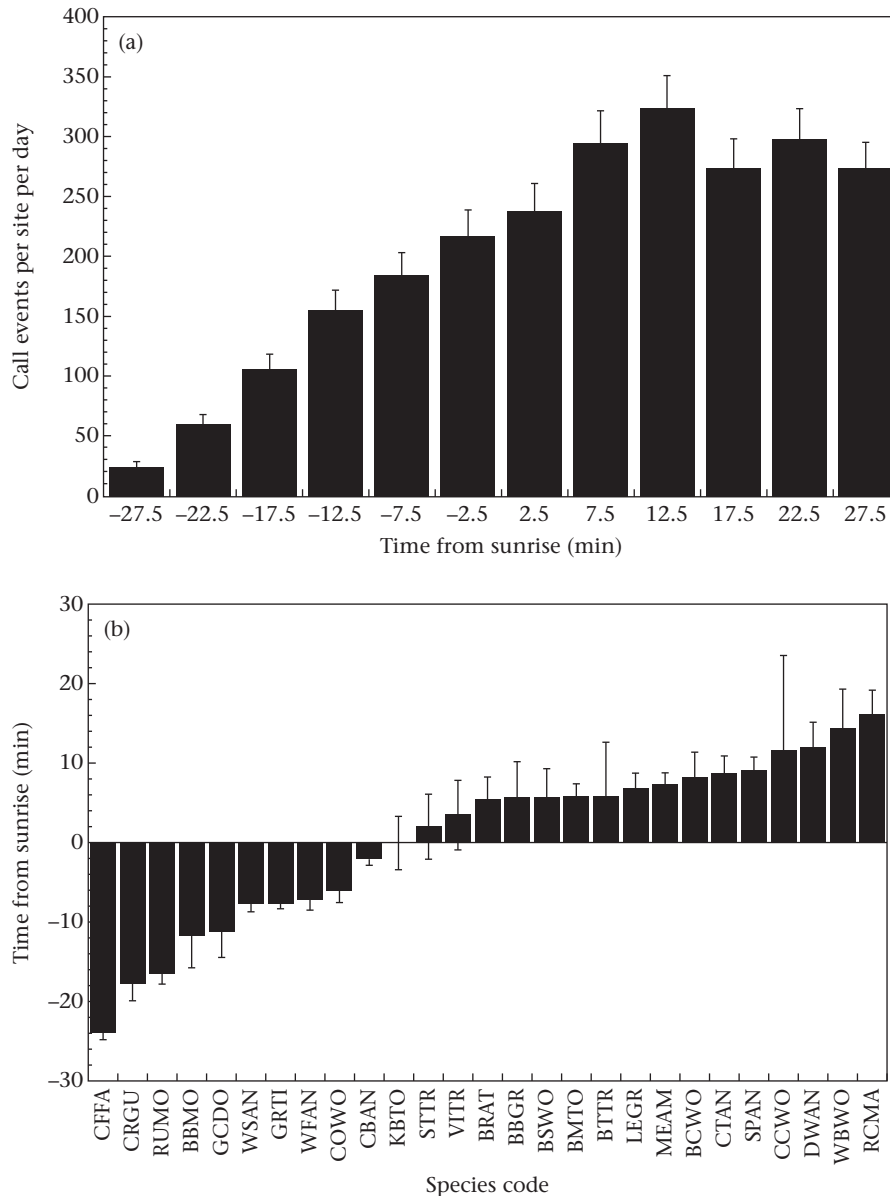


Figure 2. (a) Avian dawn chorus as defined by the number of singing events by any species averaged (\pm SE) over sites and days for each 5 min time bin. Note that calling activity peaked before the end of the recording period. (b) The first call time averaged (\pm SE) over sites and days for each species (see [Appendix, Table A1](#) for species names) displayed as time from sunrise.

(Fig. 4). These noise bands peaked at 3840 Hz, 6084 Hz and 7465 Hz. Given that the third band fell above the frequency range of birdsong, we did not consider it further. The mean background noise amplitude at the other two peaks decreased by 20.1 dB and 22.5 dB, respectively, across the 1 h sampling period. Background noise amplitudes of frequencies adjacent to these main peaks (3495–4271 Hz and 5739–6472 Hz) also decreased over the 1 h recording period by more than 8 dB. In contrast, nonavian noise was on average 2.8 dB higher at the end of the recording for all frequencies below 3 kHz. Because we could not always find a 5 s window in each 5 min bin without any bird vocalizations, the presence of bird sounds in later bins could explain why the over all amplitude of lower-frequency sounds increased over time. Twenty of the 27 birds had vocalizations with peak frequencies below 3 kHz.

The seven species with songs above 3 kHz experienced a pronounced temporal change in background noise during the dawn period and this was especially true of four species whose peak

frequencies fell into one of the two aforementioned noise bands. These species had the lowest noise difference value of all species when noise at first call time was compared to the average noise over the entire morning. These four species were the spotted antbird, *Hylophylax naevioides*, dot-winged antwren, *Microrhopias quixensis*, and black-cheeked woodpecker, *Melanerpes pucherani*, in the first band (peak at 3840 Hz) and the red-capped manakin in the second band (peak at 6084 Hz).

What Predicts Time of First Call?

First call time was predicted best by a model that included peak frequency, background noise difference, singing location, and an interaction between singing location and noise difference (Table 2). The over all model fit was highly significant (GLM: $F_{4,22} = 23.04$, $P < 0.0001$, $R^2 = 0.807$, $AICc = 234$). The next best model had an $AICc$ that was larger by 2.6 (see [Supplementary Table S4](#) for rankings of the top 10 models) and differed from the best model only by

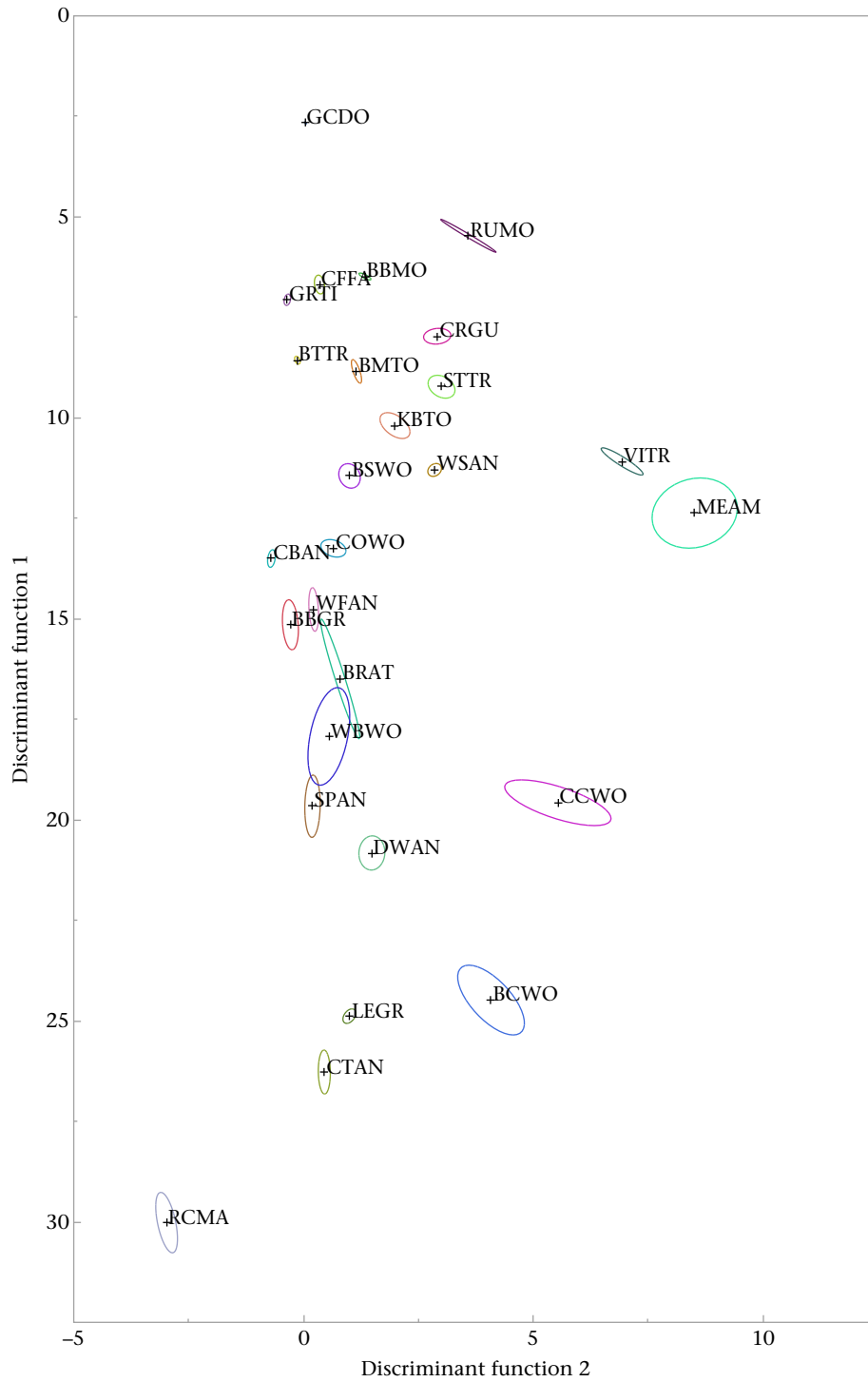


Figure 3. Centroids with 95% confidence intervals plotted for the first two discriminant functions from a quadratic discriminant function analysis using peak frequency, song complexity and song rate for 477 songs from 27 different bird species (see Appendix, Table A1 for species names).

Table 1
Variance explained and standardized coefficients for discriminant functions using three acoustic variables on 477 songs by 27 avian species

Discriminant function	Variance explained	Peak frequency	Bandwidth/duration	Notes/duration
DF1	70.8	1.11	-0.31	0.49
DF2	18.0	-0.13	0.66	0.62
DF3	11.1	0.003	0.82	-0.77

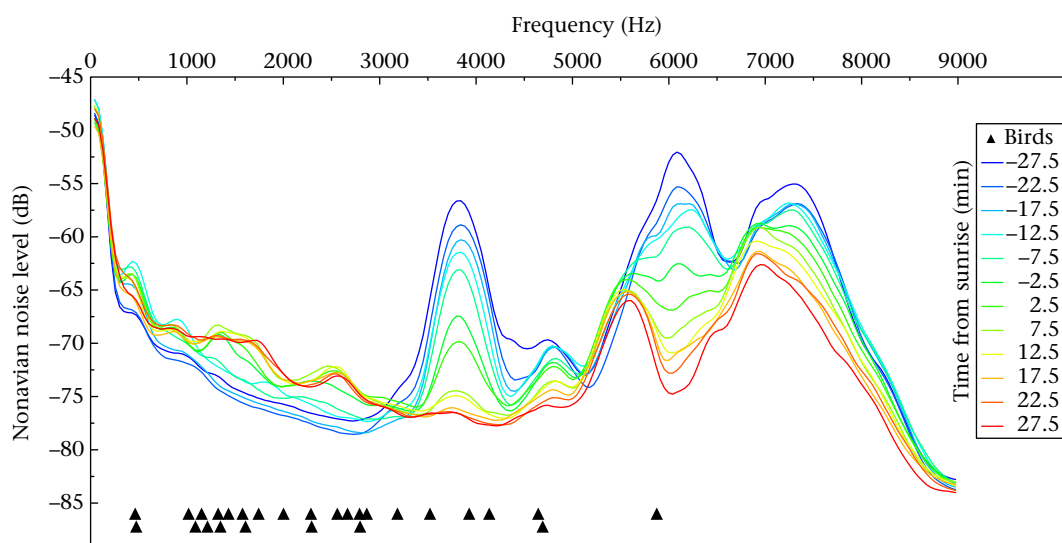


Figure 4. Nonavian noise level at different frequencies up to 9 kHz. Each line displays the average background noise colour-coded for each 5 min time interval from 30 min before until 30 min after sunrise. Black triangles indicate peak frequency of songs from the 27 bird species recorded. Amplitudes of nonavian noise are given as negative values relative to the maximum input of the recording units.

inclusion of a nonsignificant interaction term between noise difference and peak frequency. Models that included diet had AICc differences larger than 6 while those including body mass had AICc values larger than 10. Thus, neither diet nor body mass contributed to first call time prediction. The relationships between first call time and each factor in the best model are illustrated in Fig. 5. Birds that produced high-frequency songs started singing later in the morning (Fig. 5a). Although song location by itself was not significant, it was included in the best-fitting model because the interaction between song location and noise difference was significant (Table 2). This interaction was present because birds singing from the canopy exhibited a positive relationship between first call time and noise difference while birds singing below the canopy exhibited a negative relationship between first call time and noise difference (Fig. 5b). Thus, birds singing below the canopy appear to delay the start of their singing to reduce interference by nonavian noise.

Response to Cicada Playbacks

Comparison of the number of songs recorded during a playback to the number counted before the playback revealed a significant difference for three of seven common species. Paired *t* tests revealed that cocoa woodcreepers ($t_{27} = 2.19$, $P = 0.037$), chestnut-backed antbirds, *Myrmeciza exsul* ($t_{30} = 3.18$, $P = 0.003$) and white-flanked antwrens ($t_{21} = 3.73$, $P = 0.001$) produced fewer songs during playbacks than before the playbacks (Fig. 6a). In contrast, comparison of the number of songs recorded after a playback to the number counted before the playback revealed no effect for any

Table 2

Parameter estimates for best-fitting weighted model to predict first call time in 27 avian species

Variable	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	-16.23	2.17	-7.47	<0.0001
Location	2.09	1.11	1.87	0.0751
Noise difference	2.95	0.55	5.38	<0.0001
Peak frequency	0.01	0.00	7.10	<0.0001
Location * noise difference	-2.28	0.55	-4.18	0.0004

Significant outcomes are shown in bold.

species (Table 3), which indicates that the playback had no lingering effects. The three species that decreased singing activity during playbacks had songs with peak frequencies in the range covered by the cicada playback (cocoa woodcreeper: 2294 Hz; chestnut-backed antbird: 2561 Hz; white-flanked antwren: 2666 Hz) (Fig. 6b; see also Fig. 1, where all three species and cicada calls are displayed).

In addition, mixed model ANOVA on songs recorded per day per site revealed that cicada playbacks significantly altered the calling activity of collared forest-falcons. At sites and days with playbacks, forest-falcon calling was reduced by 78% compared with sites and days without playbacks (Supplementary Table S5). Singing activity of western slaty antshrikes, *Thamnophilus atrinucha*, was also reduced, but this effect was not significant after adjusting alpha by the sequential Bonferroni procedure. Calling events per day were not altered by cicada playbacks for any other species (Supplementary Table S5).

DISCUSSION

In this study we used observational and experimental approaches to identify factors that influence temporal patterns in the dawn chorus of a Neotropical bird assemblage. We found that each species in the chorus exhibited distinct start times that were consistent across sites and days. Over all, our results indicate that species call at different times to increase the active space of their vocalizations. Thus, our evidence supports a noise-avoidance version of the acoustic transmission hypothesis. But, rather than avoid other species by calling at different times, we found that birds with high-frequency vocalizations began singing at similar times later in the morning. Unexpectedly, the later start times of the high-frequency species corresponded to periods when high-frequency ambient noise declined and, therefore, allowed these species to increase their signal active space. Playbacks of cicada calling bouts confirmed that those species with songs that overlap in frequency with these insects actively reduced their singing activity during playbacks. In contrast, birds that sang below the frequency range of the cicadas did not change their calling activity during a playback, although one species, the collared forest-falcon, appeared to avoid calling at sites where playbacks were conducted. Together these

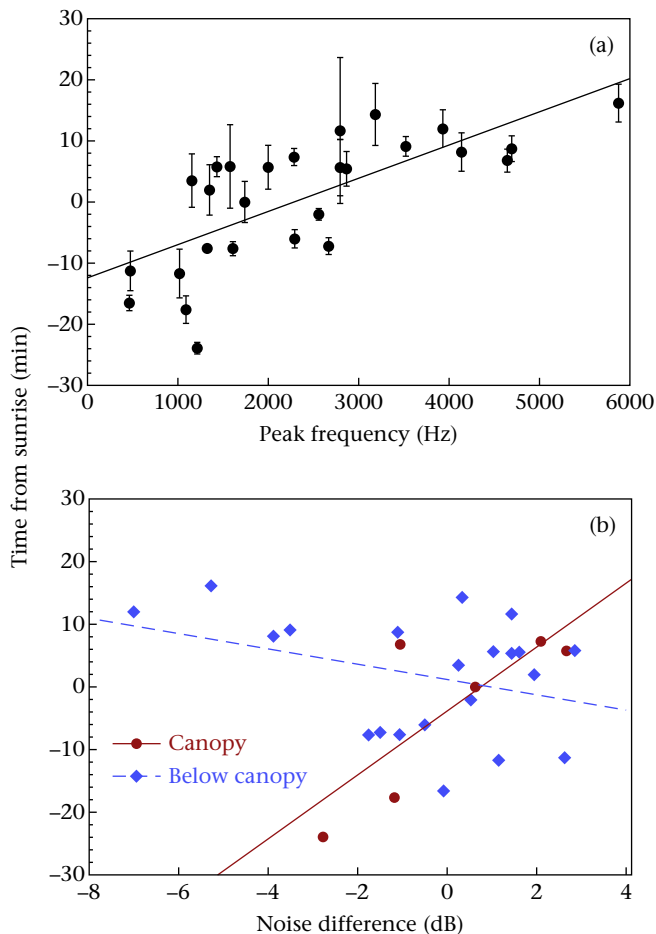


Figure 5. First call time measured as minutes from sunrise plotted against (a) peak frequency of each species and (b) the difference between background noise at first call time and over all average background noise for the 1 h period. Background noise values were calculated at each species' peak frequency band. Each point represents the mean over all days and sites (\pm SE) per species. Negative noise values indicate that birds started singing at times when ambient noise level at their songs' peak frequency was lower than the rest of the recording period. Singing location is displayed as either in the canopy (circles, solid line) or below (triangles, dashed line) the canopy. See [Table 2](#) for the parameter estimates associated with these variables.

results suggest that call start times are timed to minimize interference from ambient noise at matching frequencies, most notably from nocturnal insects.

We found no evidence in support of the other two hypotheses for explaining call start times. The inefficient foraging hypothesis suggests that birds singing higher in the canopy would start singing earlier due to higher light levels. Location of singing birds was found to matter, but not as predicted by this hypothesis. We found that birds singing below the canopy exhibited a negative relationship between first call time and background noise difference, resulting in less interference with frequency-matched noise for birds with later start times. In contrast, canopy-dwelling species showed a positive relationship between call time and noise difference, indicating that canopy species that call early experience less noise interference. We found no influence of body size on the time that each species started to sing, as was predicted by the energy stochasticity hypothesis. We suspect this hypothesis may be more suitable for explaining the timing of the dawn chorus by an individual (with regard to individual condition or weather) than for explaining interspecific differences.

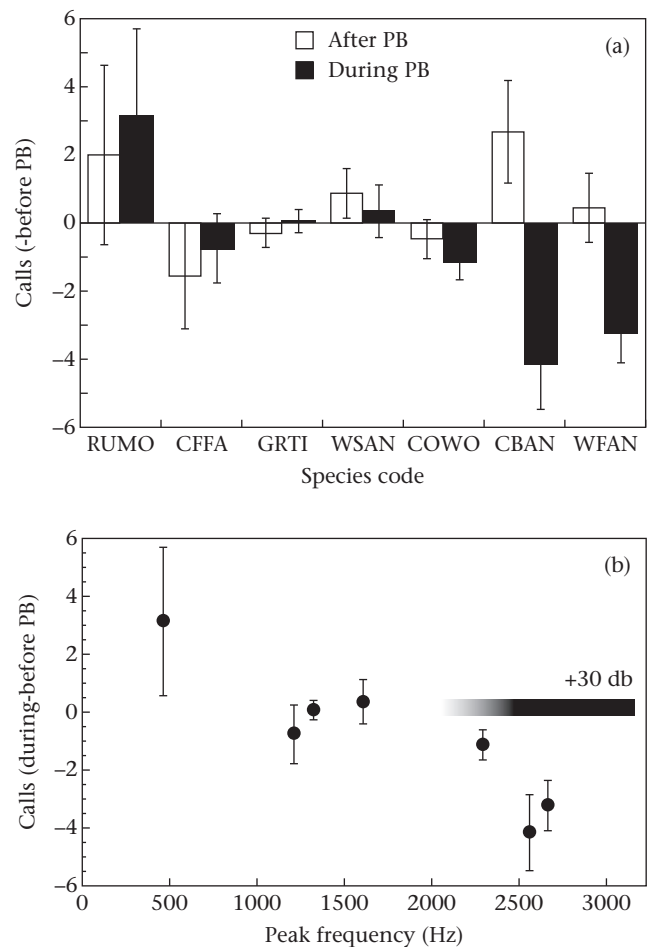


Figure 6. (a) Effect of 1 min cicada playbacks on singing behaviour of seven common birds represented as the average (\pm SE) number of songs counted 1 min during or after the playback (PB), expressed as a difference from the number counted 1 min before the playback. (b) Songs counted during playbacks minus songs counted before playbacks, plotted against peak frequency of songs, with the frequencies covered by the cicada playback illustrated by a gradient bar. For species names see [Appendix, Table A1](#).

Do Birds Partition Acoustic Space?

Similar to our findings, high levels of temporal and spectral overlap have previously been reported for avian participants in Neotropical dawn chorus ([Luther, 2009](#); [Planqué & Slabbekoorn, 2008](#)). By contrast, at finer spatiotemporal scales and with smaller numbers of species, evidence of acoustic dispersion has been found amongst some members of avian assemblages ([Ficken, Ficken, & Hailman, 1974](#); [Knapton, 1987](#); [Luther, 2009](#); [Planqué & Slabbekoorn, 2008](#); [Popp, Ficken, & Reinartz, 1985](#)). [Luther \(2009\)](#) found that species in an Amazonian bird assemblage singing in the same 30 min interval and in the same forest stratum were more acoustically dispersed in comparison to those singing in different 30 min periods of the morning. Similarly, [Planqué and Slabbekoorn \(2008\)](#) found lower realized competition for acoustic active space and reduced fine-scale temporal overlap between some species pairs in another Amazonian bird assemblage. They concluded that species whose call bandwidth falls within the most heavily used frequency range actively avoid overlap with each other. These results suggest that temporal partitioning of songs may only occur in communities or among conspecifics with high realized competition for acoustic space. In our study the temporal overlap between species suggests that interspecific competition for acoustic space

Table 3Paired *t* test results for songs of avian species counted before, during or after 1 min of cicada playbacks, and ordered by peak frequency

Species	Peak frequency (Hz)	During—before		After—before	
		<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Rufous motmot	464	1.22	0.244	0.76	0.461
Collared forest-falcon	1214	−0.74	0.471	−1.01	0.332
Great tinamou	1324	0.17	0.861	−0.69	0.489
Western slaty antshrike	1608	0.45	0.656	1.19	0.247
Cocoa woodcreeper	2294	−2.19	0.037	−0.81	0.424
Chestnut-backed antbird	2561	−3.18	0.003	1.78	0.086
White-flanked antwren	2666	−3.73	0.001	0.45	0.661

Significant outcomes are shown in bold.

within this avian community may not be intense during the dawn chorus, perhaps because species avoid masking or interference by using unique spectrotemporal features in their songs. The low acoustic competition observed on BCI may also be a consequence of the over all low avian species diversity on this man-made island. Birds may also reduce acoustic overlap by utilizing low duty cycle songs (i.e. by giving repeated notes of short duration after periods of silence). However, given the number of species singing at the peak of the chorus, active temporal avoidance among all species would be difficult, if not impossible (e.g. Fig. 1).

Do Birds Avoid Nonavian Noise?

In general terms our results are consistent with the acoustic transmission hypothesis in that we found evidence of temporal avoidance of nonavian noise produced by insects. This hypothesis is usually invoked to account for the optimization of acoustic signals based on habitat structure; however, we found instead that nonavian biogenic noise (biophony) may play an important role in determining the timing of the dawn chorus. In the tropics, insects create a large amount of nonavian noise that falls within the frequency range used by some birds for acoustic communication. Our findings indicate that birds that use high-frequency calls or songs join the dawn chorus later than species calling at low frequencies. Those species singing at high frequencies do not begin singing until nocturnal insect noise has decreased in the morning.

Analysis of ambient noise at our site revealed a notable decrease (−20 dB) in background noise, corresponding mostly to a decrease in insect noise at 3.8 kHz and 6.1 kHz at dawn. This probably corresponded to a decrease in background noise from cricket or katydid species, which are known to have narrow-banded calls with dominant frequencies ranging from 3 to 9 kHz (Schmidt, Römer, & Riede, 2013). To avoid masking by nocturnal insects in their frequency range, birds may shift their call start times to periods of the morning when ambient noise at their peak frequency is lowest. Among the species recorded within the frequency range of the nocturnal insects, four species (spotted antbird, dot-winged antwren, black-cheeked woodpecker and red-capped manakin) began singing during time periods when ambient noise within their peak frequency range was at its minimum. Calling activity of crickets is mostly restricted to the night, peaks between 1800 hours and midnight, and declines subsequently, with katydids being the main source of nocturnally produced acoustic signals (Diwakar & Balakrishnan, 2007; Lang, Kalko, Römer, Bockholdt, & Dechmann, 2006; Lang et al., 2005). On BCI, Lang et al. (2006) found that background noise drops off at sunrise and quickly reaches a daytime level of 30–50 dB SPL below average night-time levels. By delaying their participation in the dawn chorus, birds with high-frequency songs avoid interference from nocturnal insects, effectively increasing the active space of their song. In addition, waiting for this frequency window to open may be particularly advantageous for birds singing at high frequencies, as higher-frequency

songs suffer greater attenuation in tropical forest habitats (Marten, Quine, & Marler, 1977; Morton, 1975). In contrast to the decrease in high-frequency noise, ambient noise at lower frequencies (from 200 to 3000 Hz) tended to increase approximately 5 dB during our 1 h recordings (Fig. 4). Thus, those birds that join the dawn chorus early may also reduce interference from biotic noise caused by, for example, howler monkeys and other birds, such as parrots.

A variety of effects of abiotic noise on avian singing have been reported. For example, Ryan and Brenowitz (1985) found that birds in nonforest habitats in Gamboa, Panama avoided singing during times of the day when noise from wind was at its peak. More recently, effects of anthropogenic noise on bird acoustic communication have been noted. Along with detecting spectral changes in the acoustic properties (frequency, amplitude) of bird vocalizations in urban environments (Brumm, 2004; Slabbekoorn & den Boer-Visser, 2006), some studies have reported shifts in the timing of bird vocalizations in these environments (Fuller et al., 2007; Gil, Honarmand, Pascual, Pérez-Mena, & Macías Garcia, 2015; Nordt & Klenke, 2013). For example, Fuller et al. (2007) found that European robins, *Erithacus rubecula*, initiate dawn chorus earlier in environments with louder anthropogenic ambient noise, after controlling for the effect of light pollution. Similarly, Gil et al. (2015) found that bird communities near airports shifted their songs earlier than those in neighbouring areas and these shifts were larger in species whose normal singing times overlapped with periods of aircraft noise. In contrast, examples of biotic noise influencing avian communication are rare. Slabbekoorn and Smith (2002) found differences in the minimum frequency of little greenbul song, *Andropadus virens*, across populations, which were associated with habitat-dependant shifts in biogenic noise levels in their frequency range. Additionally, Kirschel et al. (2009) reported that green hylia, *Hylia prasina*, sang at lower frequencies at sites with insect noise. As with anthropogenic noise, insect noise can alter the acoustic landscape and select for behaviours or acoustic properties that enable effective communication within avian communities.

Effect of Cicada Playbacks

To determine whether birds in the dawn chorus would actively alter their calling behaviour in response to temporary insect noise, we conducted cicada playbacks. Two different strategies were employed by species when presented with cicada playbacks. One species reduced its calling activity at sites with playbacks (collared forest-falcons; Supplementary Table S5). By contrast, three species singing in the same frequency range of cicadas reduced the rate at which they called during playbacks (cocoa woodcreeper, chestnut-backed antbird and white-flanked antwren; Fig. 6a) compared to calling before the playback. These qualitatively different responses probably have different causes. The decrease in call activity by collared forest-falcons at sites with playbacks suggests that these

birds avoid noise by moving to other parts of their range where that noise is less common and communication can be more effective. Collared forest-falcons can range over 1000 ha (Thorstrom, 2007). In contrast, a reduction of calling activity only during playbacks by the three species with song frequencies that overlap cicada bouts could represent a strategy to mitigate losses associated with calling (such as energy, time lost from other activities or increased predation risk) when faced with broadband noise that could temporarily reduce communication effectiveness drastically. Such flexible calling behaviour could be an important strategy for species with small home ranges. Nevertheless, these short-term behavioural responses to cicada playbacks indicate that some birds actively avoid call masking by nonavian noise.

Similar short-term responses to noise have been observed in other species. Strawberry poison-dart frogs, *Oophaga pumilio*, show a similar inhibitory response to cicada choruses and respond less to playbacks of conspecifics when cicadas are calling in the background (Paez, Bock, & Rand, 1993). To avoid masking by acoustically dominant heterospecifics, birds in temperate forests have been found to insert their songs directly after songs of dominant species (Ficken et al., 1974; Popp et al., 1985). To mitigate the influence of temporary ambient noise, two additional mechanisms have been observed in avian species: the addition of extra syllables in a call series (e.g. Lengagne, Aubin, Lauga, & Jouventin, 1999; Potash, 1972) or amplitude modulation of vocalizations, termed the Lombard effect (e.g. Brumm, 2004; Brumm & Todt, 2002). To our knowledge, neither of these short-term mechanisms to avoid interference has been examined with respect to insect noise before.

Although these results suggest that nonavian biological noise can have important effects on avian acoustic communication, extrapolating from these playback results should be done with caution. We only counted species that sang frequently and whose songs could be detected in spectrograms during cicada calling bouts. Species that called less often would be difficult to hear or identify in spectrograms during playback periods. Therefore, we cannot conclude that all species with high-frequency songs actively avoid cicada noise. In addition, our methods only monitored the behaviour of senders and the effect of noise on signal active space. The responsiveness of receivers could also be an important factor influencing sender calling behaviour in a noisy environment and warrants further investigation.

Conclusions

The acoustic transmission hypothesis has most often been used to explain why dawn is a favourable climatic period of the day to produce vocalizations. This hypothesis has not previously been invoked to explain interspecific variation in when individuals should join a dawn chorus. By considering the possibility that biotic noise varies by frequency over time, especially at dawn, we discovered that the time when a bird species joins the dawn chorus can be predicted by the frequency of its song and associated temporal noise profile. We did not find evidence of acoustic avoidance of avian noise, as we had initially predicted, possibly because the songs of most species have sufficiently unique spectrotemporal features to make them distinguishable within the chorus of this community. Instead, we found evidence of nonavian noise avoidance during dawn chorus. In particular, birds with high-frequency songs began singing later once the noise profile of those frequency ranges had decreased due to a reduction in acoustic signals produced by insects. Birds with low-frequency songs joined the chorus earlier before ambient noise at their frequencies increased at dawn. Active avoidance of insect noise was demonstrated by our playback experiment in which birds that call in the frequency range of emerald cicadas significantly reduced their calling activity

during playbacks of cicada calls. These results highlight the potential importance of the entire tropical forest acoustic community in shaping the avian dawn chorus. Given that this study only assessed the influence of nonavian noise on the dawn chorus at one location and period, considering additional sites and seasons with different noise profiles would provide further insight into the influence of nonavian noise on the acoustic properties of avian assemblages.

Acknowledgments

This work was supported by the University of Maryland Graduate School and the Institute for Neurobiology at the University of Tübingen. We thank Gail Patricelli, two anonymous referees and the members of the Animal Communication course for helpful suggestions.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2015.12.003>.

References

- Allard, H. A. (1930). The first morning song of some birds of Washington, District of Columbia; its relation to light. *American Naturalist*, *64*, 436–469.
- Armstrong, E. A. (1963). Songs for all occasions: significance of singing as a part of bird behavior. *Animal Kingdom*, *66*, 27–29.
- Berg, K. S., Brumfield, R. T., & Apanius, V. (2006). Phylogenetic and ecological determinants of the Neotropical dawn chorus. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 999–1005.
- Brenowitz, E. A. (1982). The active space of red-winged blackbird song. *Journal of Comparative Physiology*, *147*, 511–522.
- Brown, T. J., & Handford, P. (2003). Why birds sing at dawn: the role of consistent song transmission. *Ibis*, *145*, 120–129.
- Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology*, *73*, 434–440.
- Brumm, H., & Slabbekoorn, H. (2005). Acoustic communication in noise. *Advances in the Study of Behavior*, *35*, 151–209.
- Brumm, H., & Todt, D. (2002). Noise-dependent song amplitude regulation in a territorial songbird. *Animal Behaviour*, *63*, 891–897.
- Diwakar, S., & Balakrishnan, R. (2007). The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: call diversity and diel calling patterns. *Bioacoustics*, *16*, 113–135.
- Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *American Naturalist*, *139*, 125–153.
- Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *340*, 215–225.
- Ficken, R. W., Ficken, M. S., & Hailman, J. P. (1974). Temporal pattern shifts to avoid acoustic interference in singing birds. *Science*, *183*, 762–763.
- Fuller, R. A., Warren, P. H., & Gaston, K. J. (2007). Daytime noise predicts nocturnal singing in urban robins. *Biology Letters*, *3*, 368–370.
- Gil, D., Honarmand, M., Pascual, J., Pérez-Mena, E., & Macías García, C. (2015). Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behavioral Ecology*, *26*, 435–443.
- Henwood, K., & Fabrick, A. (1979). A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. *American Naturalist*, *114*, 260–274.
- Holdridge, L. R. (1967). *Life zone ecology* (Rev. ed.). San José, Costa Rica: Tropical Science Center.
- Hutchinson, J. M. (2002). Two explanations of the dawn chorus compared: how monotonically changing light levels favour a short break from singing. *Animal Behaviour*, *64*, 527–539.
- Kacelnik, A. (1979). The foraging efficiency of great tits (*Parus major* L.) in relation to light intensity. *Animal Behaviour*, *27*, 237–241.
- Kirschel, A. N. G., Blumstein, D. T., Cohen, R. E., Buermann, W., Smith, T. B., & Slabbekoorn, H. (2009). Birdsong tuned to the environment: green hylia song varies with elevation, tree cover, and noise. *Behavioral Ecology*, *20*, 1089–1095.
- Knapton, R. W. (1987). Intraspecific avoidance and interspecific overlap of song series in the eastern meadowlark. *Auk*, *104*, 775–779.
- Krams, I. (2001). Communication in crested tits and the risk of predation. *Animal Behaviour*, *61*, 1065–1068.
- Lang, A. B., Kalko, E. K. V., Römer, H., Bockholdt, C., & Dechmann, D. K. N. (2006). Activity levels of bats and katydid in relation to the lunar cycle. *Oecologia*, *146*, 659–666.

- Lang, A. B., Teppner, I., Hartbauer, M., & Römer, H. (2005). Predation and noise in communication networks of Neotropical katydids. In P. K. McGregor (Ed.), *Animal communication networks* (pp. 152–169). Cambridge, U.K.: Cambridge University Press.
- Lengagne, T., Aubin, T., Lauga, J., & Jouventin, P. (1999). How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? *Proceedings of the Royal Society B: Biological Sciences*, 266, 1623–1628.
- Leopold, A., & Eynon, A. E. (1961). Avian daybreak and evening song in relation to time and light intensity. *Condor*, 63, 269–293.
- Luther, D. (2009). The influence of the acoustic community on songs of birds in a Neotropical rainforest. *Behavioral Ecology*, 20, 864–871.
- Luther, D., & Gentry, K. (2013). Sources of background noise and their influence on vertebrate acoustic communication. *Behaviour*, 150, 1045–1068.
- Marten, K., Quine, D., & Marler, P. (1977). Sound transmission and its significance for animal vocalization II. Tropical forest habitats. *Behavioral Ecology and Sociobiology*, 2, 291–302.
- McNamara, J., Mace, R., & Houston, A. (1987). Optimal daily routines of singing and foraging in a bird singing to attract a mate. *Behavioral Ecology and Sociobiology*, 20, 399–405.
- Morton, E. S. (1975). Ecological sources of selection on avian sounds. *American Naturalist*, 109, 17–34.
- Nischk, F., & Riede, K. (2001). Bioacoustics of two cloud forest ecosystems in Ecuador compared to a lowland rainforest with special emphasis on singing cricket species. In J. Nieder, & W. Barthlott (Eds.), *Epiphytes and canopy fauna of the Otongán rainforest (Ecuador)* (Vol. 2, pp. 217–242). Norderstedt, Germany: Books on Demand GmbH.
- Nordt, A., & Klenke, R. (2013). Sleepless in town—drivers of the temporal shift in dawn song in urban European blackbirds. *PLoS One*, 8, e71476.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R., et al. (2013). *Vegan: Community ecology package (Version 2.3–1)*. [http://github.com/vegandevs/vegan](http://cran.r-project.org).
- Paez, V. P., Bock, B. C., & Rand, A. S. (1993). Inhibition of evoked calling of *Dendrobates pumilio* due to acoustic interference from cicada calling. *Biotropica*, 25, 242–245.
- Planqué, R., & Slabbekoorn, H. (2008). Spectral overlap in songs and temporal avoidance in a Peruvian bird assemblage. *Ethology*, 114, 262–271.
- Popp, J. W., Ficken, R. W., & Reinartz, J. A. (1985). Short-term temporal avoidance of interspecific acoustic interference among forest birds. *Auk*, 102, 744–748.
- Potash, L. M. (1972). A signal detection problem and possible solution in Japanese quail (*Coturnix coturnix japonica*). *Animal Behaviour*, 20, 192–195.
- Rodriguez, A., Gasc, A., Pavoine, S., Grandcolas, P., Gaucher, P., & Sueur, J. (2014). Temporal and spatial variability of animal sound within a Neotropical forest. *Ecological Informatics*, 21, 133–143.
- Ryan, M. J., & Brenowitz, E. A. (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist*, 126, 87–100.
- Schmidt, A. K. D., Römer, H., & Riede, K. (2013). Spectral niche segregation and community organization in a tropical cricket assemblage. *Behavioral Ecology*, 24, 470–480.
- Slabbekoorn, H. (2004). Habitat-dependent ambient noise: consistent spectral profiles in two African forest types. *Journal of the Acoustical Society of America*, 116, 3727–3733.
- Slabbekoorn, H., & den Boer-Visser, A. (2006). Cities change the songs of birds. *Current Biology*, 16, 2326–2331.
- Slabbekoorn, H., & Smith, T. B. (2002). Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. *Evolution*, 56, 1849–1858.
- Stiles, F. G., Skutch, A. F., & Gardner, D. (1989). *A guide to the birds of Costa Rica* (Rev. ed.). London, U.K.: Christopher Helm.
- Thomas, R. J., Székely, T., Cuthill, I. C., Harper, D. G. C., Newson, S. E., Frayling, T. D., et al. (2002). Eye size in birds and the timing of song at dawn. *Proceedings of the Royal Society B: Biological Sciences*, 269, 831–837.
- Thorstrom, R. (2007). Home ranges of barred (*Micrastur ruficollis*) and collared (*M. semitorquatus*) forest-falcons during the breeding season in Tikal National Park, Guatemala. *Ornitología Neotropical*, 18, 395–405.
- Wiley, R. H. (1994). Errors, exaggeration, and deception in animal communication. In L. Real (Ed.), *Behavioral mechanisms in ecology* (pp. 157–189). Chicago, IL: University of Chicago Press.
- Wiley, R. H. (2006). Signal detection and animal communication. *Advances in the Study of Behavior*, 36, 217–247.
- Willis, E. O. (1974). Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecological Monographs*, 44, 153–169.
- Wood, W. E., & Yezerinac, S. M. (2006). Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk*, 123, 650–659.

APPENDIX

Table A1

Common names, Latin names and alpha codes for the 27 avian species recorded at six sites on Barro Colorado Island, Panama

Common name	Code	Latin name
Grey-chested dove	GCDO	<i>Leptotila cassinii</i>
Rufous motmot	RUMO	<i>Baryphthengus martii</i>
Broad-billed motmot	BBMO	<i>Electron platyrhynchum</i>
Collared forest-falcon	CFFA	<i>Micrastur semitorquatus</i>
Crested guan	CRGU	<i>Penelope purpurascens</i>
Blue-black grosbeak	BBGR	<i>Cyanocompsa cyanoides</i>
Wedge-billed woodcreeper	WBWO	<i>Glyphorhynchus spirurus</i>
Black-striped woodcreeper	BSWO	<i>Xiphorhynchus lachrymosus</i>
Cocoa woodcreeper	COWO	<i>Xiphorhynchus susurrans</i>
Red-capped manakin	RCMA	<i>Ceratopipra mentalis</i>
Checker-throated antwren	CTAN	<i>Epinecrophylax fulviventris</i>
Spotted antbird	SPAN	<i>Hylophylax naevioides</i>
Dot-winged antwren	DWAN	<i>Microrhopias quixensis</i>
Chestnut-backed antbird	CBAN	<i>Myrmeciza exsul</i>
White-flanked antwren	WFAN	<i>Myrmotherula axillaris</i>
Western slaty antshrike	WSAN	<i>Thamnophilus atrinucha</i>
Bright-rumped attila	BRAT	<i>Attila spadiceus</i>
Lesser greenlet	LEGR	<i>Hylophilus decurtatus</i>
Crimson-crested woodpecker	CCWO	<i>Campephilus melanoleucus</i>
Black-cheeked woodpecker	BCWO	<i>Melanerpes pucherani</i>
Black-mandibled toucan	BMTO	<i>Ramphastos ambiguus</i>
Keel-billed toucan	KBTO	<i>Ramphastos sulfuratus</i>
Mealy parrot	MEAM	<i>Amazona farinosa</i>
Great tinamou	GRTI	<i>Tinamus major</i>
Slaty-tailed trogon	STTR	<i>Trogon massena</i>
Black-throated trogon	BTTR	<i>Trogon rufus</i>
Violaceous trogon	VITR	<i>Trogon violaceus</i>